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CONTRIBUTIONS TO ENTOMOLOGY

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Research Article

First Eumastacoidea and new Locustopsidae (Orthoptera: Caelifera) from the Crato Formation of Brazil

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Abstract

The first genus and species of Eumastacoidea from the Lower Cretaceous Crato Formation of northeastern Brazil is described. *Cratomastax mariellaae* **gen. et sp. nov.** is reported from a relatively well-preserved specimen, with the wings, head, and metathoracic leg aspects in good condition. It is assigned to the Eumastacoidea based on its forewing venation feature, with M and CuA + CuPaα fused. Due to the presence of two branches of M + CuA, it may be allied to Chorotypidae, but the forewing venation of other families of Eumastacoidea is not sufficiently known to confidently exclude it from these taxa. Additionally, a second species of *Aestuacrida* is described from the Crato Formation. *Aestuacrida mikronaulion* **sp. nov.** is significantly larger than *A. stereofemoris* Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, 2025, and its wing venation is more fully preserved. The new species suggests that *Aestuacrida* belongs to the subfamily Pseudoacridinae, increasing the diversity of this recently established taxon. Lastly, a new specimen of *Locustrix gallegoi* Martins-Neto, 2003, is reported. Individuals of this genus appear to be rather rare, and the apomorphies of *Locustrix* Martins-Neto, 2003, were not well understood. The new specimen helps resolve this issue. *Locustrix* can now be assigned to the subfamily Locustopsinae. The genus is characterized by having two branches of M and CuA + CuPaα and a short ScP of only about 50% of the total forewing length.

Key Words

Fossil, grasshopper, monkey hopper, taxonomy

Introduction

With over 29,000 extant species, Orthoptera Olivier, 1789, is the most diverse order of polyneopteran insects (Cigliano et al. 2025). The order is traditionally divided into two major suborders: Ensifera Chopard, 1921—encompassing katydids and crickets—and Caelifera Ander, 1936, which includes short-horned grasshoppers and locusts. Both lineages have a deep evolutionary history, with definite fossil representatives of each suborder reported from the Late Permian (255.7 Ma) (Riek 1976; Bethoux et al. 2002).

During the Mesozoic (251.9–66.0 Ma), one of the most distinctive caeliferan families was Locustopsidae Handlirsch, 1906. These orthopterans resemble the extant Acridoidea Macleay, 1821, particularly in wing venation and general body shape and proportions. Locustopsidae are known from multiple fossiliferous formations worldwide, with notable occurrences in the Lower Jurassic and Lower Cretaceous deposits of Europe, particularly the

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UK (Brodie 1845; Cockerell 1916; Gorochov et al. 2006; Handlirsch 1939; Whalley 1985; Zeuner 1942) and Germany (Bode 1953; Geinitz 1880; Handlirsch 1906, 1939; Zessin 1983).

Additionally, the Lower Cretaceous Crato Formation of northeastern Brazil stands out for its exceptional preservation and taxonomic richness. Recent studies have revealed a remarkable diversity of Locustopsidae in this Konservat-Lagerstätte, with more than twice the number of genera described from this single locality compared to any other known site worldwide (Martins-Neto 1995, 1998, 2003; Nel and Jouault 2022; Schall et al. submitted). Remarkably, only the Crato assemblage contains representatives of all three subfamilies currently recognized within the family (Schall et al. submitted).

Locustopsidae are mainly characterized by their forewing venation, i.e., the number of branches of CuA + CuPaα and M. Genera within Araripelocustinae Martins-Neto, 1995, are distinguished by a simplified venation pattern, displaying a single branch of M and one to two branches of CuA + CuPaα (Gorochov et al. 2006). In contrast, Locustopsinae Handlirsch, 1906—the most speciose subfamily—typically exhibit two to three branches of M and one to three branches of CuA + CuPaα. The most recently established subfamily, Pseudoacridinae Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, submitted, is characterized by a CuA + CuPaα that extends significantly beyond its point of fusion with CuPaβ and terminates markedly closer to the wing base than in any other locustopsid.

Among extant Caelifera, the second most diverse superfamily after Acridoidea is Eumastacoidea Burr, 1899 (Cigliano et al. 2025). The fossil record of this group is dominated by isolated wing imprints, which can often be recognized by the characteristic fusion of the M and CuA veins (Zessin 2017; Schubnel et al. 2020). Nonetheless, a limited number of eumastacoid species with preserved body morphology have also been documented, primarily from amber. These specimens are generally wingless or brachypterous and may represent nymphal stages (Perez-Gelabert 1997; Husemann et al. 2025).

The classification of fossil Eumastacoidea remains problematic due to the reliance on detailed analysis of external and internal genitalia for extant taxa (Descamps 1979; Rowell and Perez-Gelabert 2006). As a result, most fossil identifications are tentative and based solely on wing venation. To date, fossil eumastacoids have been assigned to Episactidae Burr, 1899 (Perez-Gelabert et al. 1997), Eumastacidae Burr, 1899 (e.g., Zessin 2017), and Chorotypidae Stål, 1873 (Schubnel et al. 2020). However, the venation of extant representatives remains poorly characterized, and many species are brachy- or apterous, further complicating comparison with fossil material.

Until now, no formal description of a eumastacoid from the Crato Formation had been published, although the possible existence of the group was previously hypothesized by Martins-Neto (1991). More recently, Husemann et al. (2025) speculated on the presence of Eumastacoidea in South American Gondwana, based on a brachypterous specimen recovered from Burmese amber—an ecosystem with proposed Gondwanan biogeographic affinities.

In this study, we formally describe the first confirmed Eumastacoidea from the Crato Formation. Additionally, we present a new species of Locustopsidae from this unit and report a new specimen of *Locustrix gallegoi* Martins-Neto, 2003, which contributes valuable morphological data toward refining the taxonomy of the genus.

Geological setting

The Mesozoic sedimentary succession of the Araripe Basin developed within the Borborema Province, in the interior of northeastern Brazil, by the reactivation of Neoproterozoic faults in response to the opening of the South Atlantic (Matos 1992). The Early Cretaceous transitional phase of this basin is represented by the Barbalha, Crato, Ipubi, and Romualdo formations that constitute the Santana Group (Assine et al. 2014). These units encompass a mixed carbonate–evaporite–siliciclastic depositional system tract (Arai 2014; Assine et al. 2016; Varejão et al. 2016) (Fig. 1).

The Crato Formation is a succession of interbedded limestone, shale, mudstone, and sandstone and is one of the most studied units of the Araripe Basin due to its fossil content, especially the diverse flora and fauna found in the lower part of the laminated limestones known as the Nova Olinda Member (Martill et al. 2007; Santos et al. 2017; Nascimento Jr. et al. 2023). Crato strata are interpreted as a lacustrine system due to the presence of continental fauna, flora, and particular carbon and oxygen isotopic values (Heimhofer et al. 2010; Varejão et al. 2021). The Crato Formation contains abundant and exceptionally preserved fossils, including fishes, arthropods, turtles, pterosaurs, fungi, gymnosperms, and early flowering plants, making it one of the most important Cretaceous *Konservat-Lagerstätten* worldwide (Mendes et al. 2020). Among these, insects are recognized as the best-preserved fossils and thrived on the margins of a lake, or several lakes, under frequent hypersaline and alkaline conditions (Bezerra and Mendes 2024). Currently, there are two modes of insect preservation in the Crato Formation: kerogenization and pyritization (Osés et al. 2016; Bezerra et al. 2018). Kerogenized insects consist of amorphous carbon, while pyritized insects are preserved as oxyhydroxides after pyrite (Barling et al. 2020; Bezerra et al. 2021).

Paleontological works often solely reference "limestones" of the Crato Formation without specifying the carbonate unit in which the fossils are found. To address this, Corecco et al. (2022) adopted an informal nomenclature to specify the stratigraphic position of the fossils. In particular, the insects of the Crato Formation are collected in the uppermost portion of the laminated limestones, informally named "veio do besouro" (beetle vein). The absence of diagnostic microfossils or volcanic ash challenges the robust

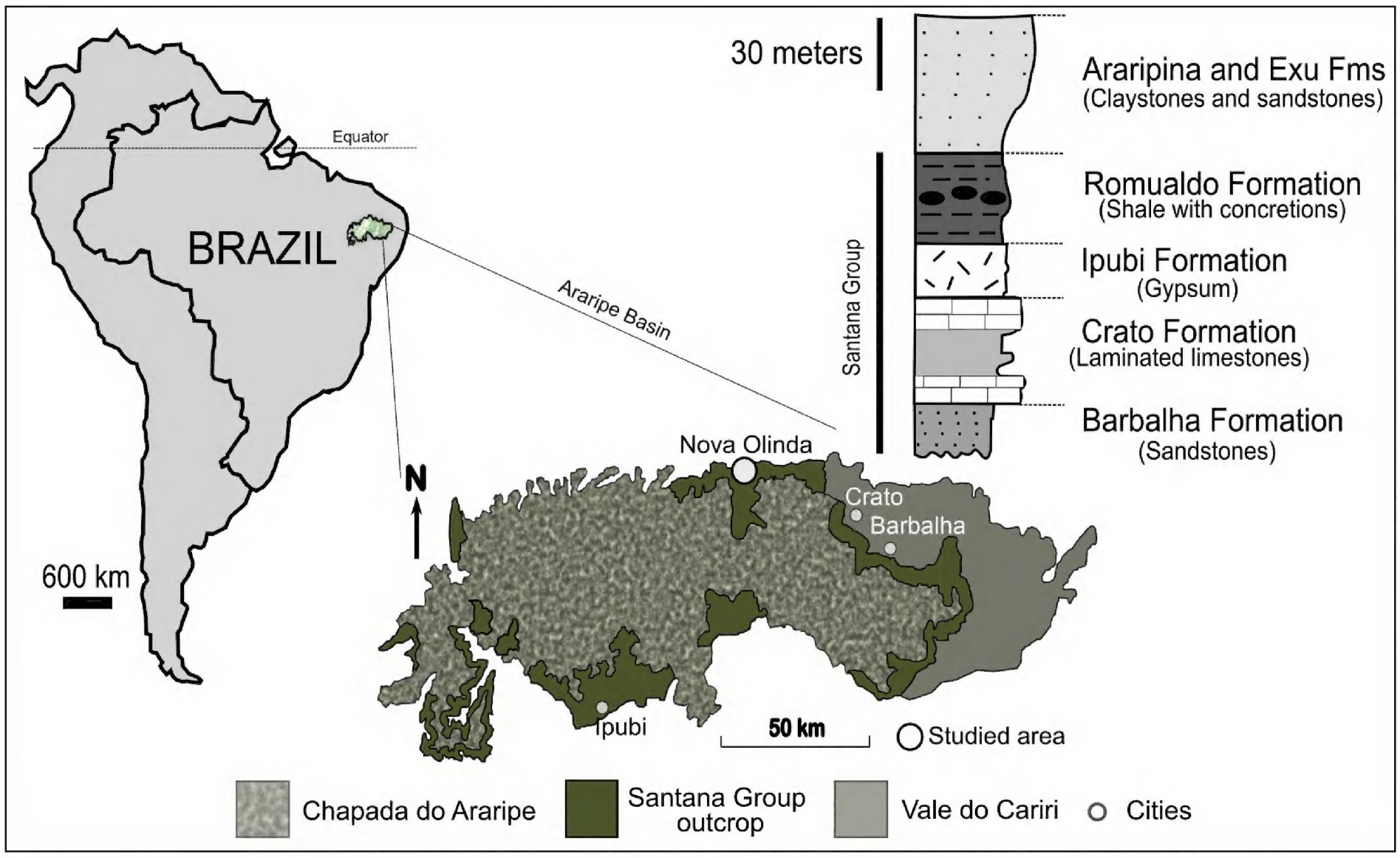

Figure 1. Geologic map and location of the Araripe Basin in northeastern Brazil.

establishment of the age of this unit. Lúcio et al. (2020) proposed a late Barremian age for this interval based on isotopic analysis. However, a series of studies based on micropaleontological data converge in placing the Crato strata in the late Aptian–early Albian interval (Coimbra et al. 2002; Heimhofer and Hochuli 2010; Arai 2014; Coimbra and Freire 2021). Arai and Assine (2020) and Melo et al. (2020), based on microfossil assemblages, consider placing the Crato Formation in the Late Aptian.

Materials and methods

Type specimens are deposited in the Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, under collection numbers MPSC 9664 and MPSC 9665. A non-type specimen is deposited in the collection of the State Museum for Natural History Karlsruhe, under collection number SMNK-PAL 76082.

Imaging of the specimens was conducted using a Keyence VHX-6000 digital microscope (MPSC 9664) and a Keyence VHX-7000 digital microscope (MPSC 9665; MH_Fossil_0066) (KEYENCE Corporation 2024, Osaka, Japan; https://www.keyence.com/). All images are composite images assembled using the stitching method. Drawings of the specimens were created in GIMP (v. 3.0.2-1) (The GIMP Team 2025; https://www.gimp.org/) by direct layer copying. Figures were assembled and modified, including scale bars and labeling, in Inkscape (v. 1.4.2) (The Inkscape Team 2025; https://inkscape.org/).

The taxonomy used in this study follows the Orthoptera Species File (Cigliano et al. 2025; https://orthoptera.speciesfile.org/). Wing venation nomenclature follows Béthoux and Nel (2002), with the following abbreviations: CP = posterior costa; ScA, ScP = anterior/posterior subcosta; R = radius; RA, RP = anterior/posterior radius; MA, MP = anterior/posterior media; CuA, CuP = anterior/posterior cubitus; CuPaα = anterior branch of the first posterior cubitus; CuPaβ = posterior branch of the first posterior cubitus; CuPb = second posterior cubitus; 1A = anterior anal vein.

Systematic paleontology

Order Orthoptera Olivier, 1789
Suborder Caelifera Ander, 1936
Superfamily Eumastacoidea Burr, 1899

Genus *Cratomastax* gen. nov.

https://zoobank.org/C6653F0A-A70E-4937-B919-A5A1217DAC0A

Type species. *Cratomastax mariellaae* sp. nov. by monotypy and present designation. Gender: feminine.

Etymology. The genus name is derived from the Crato Formation, the type deposit of the fossil, combined with "eumastax," referring to its systematic position within Eumastacoidea.

Diagnosis. As for the type species by monotypy.

Remarks. *Cratomastax* gen. nov. is attributed to Eumastacoidea based on the fusion of M and CuA

in the tegmina. Despite morphological similarities to *Paleochina duvergeri* Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020 and *P. minuta* Schubnel, Desutter-Grandcolas, Garrouste, Hervet & Nel, 2020 from the Paleocene of France (compare species remarks), we refrain from assigning *Cratomastax* gen. nov. to Chorotypidae Stål, 1873, the family of *Paleochina*, or to any other family within Eumastacoidea. The classification of fossil eumastacoids remains problematic due to the limited availability of morphological characters that define modern taxa. Extant Eumastacoidea are organized either based on molecular data (Matt et al. 2008) or on detailed examination of the external and, especially, internal genitalia (Rowell and Perez-Gelabert 2006), features that are rarely preserved in fossils. While external genitalia are occasionally visible (e.g., Husemann et al. 2025), this is not the case in *C. mariellaae* gen. et sp. nov. Although some modern Chorotypidae (e.g., *Erucius dimidiatipes* Bolívar, 1898) share a similar wing venation with *Paleochina* or *Cratomastax* gen. nov., the lack of information regarding the wing venation of the ancestors of many extant apterous or brachypterous genera across Eumastacoidea provides few opportunities for comparisons on which to base phylogenetic relationships. Because the wing venation of modern Eumastacoidea is almost unstudied, it cannot be considered a reliable character for family placement in the absence of additional corroborating morphological data. Among other fossil genera of Eumastacoidea, *Taphacris* Scudder, 1890, from the Eocene of Colorado, USA, and the Cretaceous–Eocene of China, and *Eoerianthus* Gorochov, 2012 (in Gorochov and Labandeira 2012), from the Eocene of Colorado, USA, *Cratomastax* gen. nov. can be differentiated by the much narrower space between CuPaβ and CuPb. It further differs from *Eozaenhuepfer* Zessin, 2017, from the Eocene of Denmark, which has a similarly narrow CuPaβ and CuPb space, by having one fewer branch of M, two in *E. erteboellei* Zessin, 2017, and one additional branch of RP, four in *E. erteboellei*. *Cratomastax* gen. nov. also differs from *Archaeomastax* Sharov, 1968, from the Jurassic of Kazakhstan, by having a longer ScP and ScP fused to RA, instead of reaching the costal margin as in *Archaeomastax*. This feature also distinguishes it from *Promastax* Handlirsch, 1910, from the Eocene of British Columbia, and the problematic *Promastacoides* Kevan & Wighton, 1981, from the Eocene of Alberta. It further differs from the two Eumastacoidea preserved in amber—*Paleomastacris* Perez-Gelabert, Hierro, Dominici & Otte, 1997, from Dominican amber, Miocene, and *Burmeumastax* Husemann, Schall, Uchida & Kotthoff, 2025, from Kachin amber, mid-Cretaceous—by its much larger and fully developed wings. The single type species of *Paleomastacris* is apterous, whereas the single type species of *Burmeumastax* is brachypterous (Perez-Gelabert et al. 1997; Husemann et al. 2025).

***Cratomastax mariellaae* sp. nov.**

https://zoobank.org/E10585E6-2451-448E-89DA-F7A19046FCB2

Fig. 2

Etymology. The species is named in honor of Prof. Dr. Mariella Herberstein, currently Head of the Center for Taxonomy and Morphology at the Leibniz Institute for the Analysis of Biodiversity Change (LIB), Hamburg, Germany, in recognition of her kind support of the first author's dissertation work.

Locality and horizon. Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Holotype. Unsexed specimen in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll. no. MPSC 9664. Donation from the Husemann Research Collection of Prof. Dr. Martin Husemann (collection number HC_0042) as part of the guidelines discussed at the "Brazil-German Colloquium on Paleontology: Science, Cooperation, and Diplomacy for the Future."

Diagnosis of species. Forewing length 30.2 mm. Forewing length/height 7. M and CuA fused to one branch. CuA + CuPaα and M one branched. RP with five branches. ScP long, reaching origin of RP2, fused terminally with RA. ScA reaching up to 37.2% of total wing length. 1A very long, reaching anal margin almost as far distally as CuA + CuPaα. CuPb and CuPaβ parallel to 1A but each slightly shorter. Space between 1A, CuPb, and CuPaβ narrow. Head height 6.67 mm. Eye height ca. 2.09 mm, oval-shaped and not protruding above head. Metafemur ca. 19.8 mm long, ca. 3.54 mm high. Metatibia at least 19 mm long, with distinct armature consisting of 16 + spines up to 0.83 mm long (spine length measured along dorsal line of longest spine).

Description. Wings, head, and metathoracic leg preserved up to distal metatibia. Pro-, mesothoracic leg and body fragmentary.

Forewing. Length/height-ratio 7. ScP long and narrow, 93.1% of total wing length (twl). ScA reaching costal wing margin after 37.2% of twl. ScP distally with slight upwards path, fused to RA. Space between ScP and RA 7.4% of total wing height (measured at meeting point of CuA + CuPaα reaching anal margin). Origin of RP at 52.2% of twl, slightly posterior to bifurcation of M + CuA. Space between RA and RP 12% of wing height (measured at same point as before). RP with five branches. M and CuA + CuPaα simple; bifurcation of M + CuA at 48.2% of twl. M reaching anal wing margin at 88.5% of twl. CuA + CuPaα reaching anal wing margin at 80.2% of twl. CuPaβ simple, fused to CuPb at 61.7% of twl. CuPb fused to 1A at 65.4% of twl. 1A reaching anal wing margin after 78.3% of twl. Space between 1A and CuPb and CuPaβ and CuPb narrow. All three veins run parallel. Cross vein pattern simple, except for

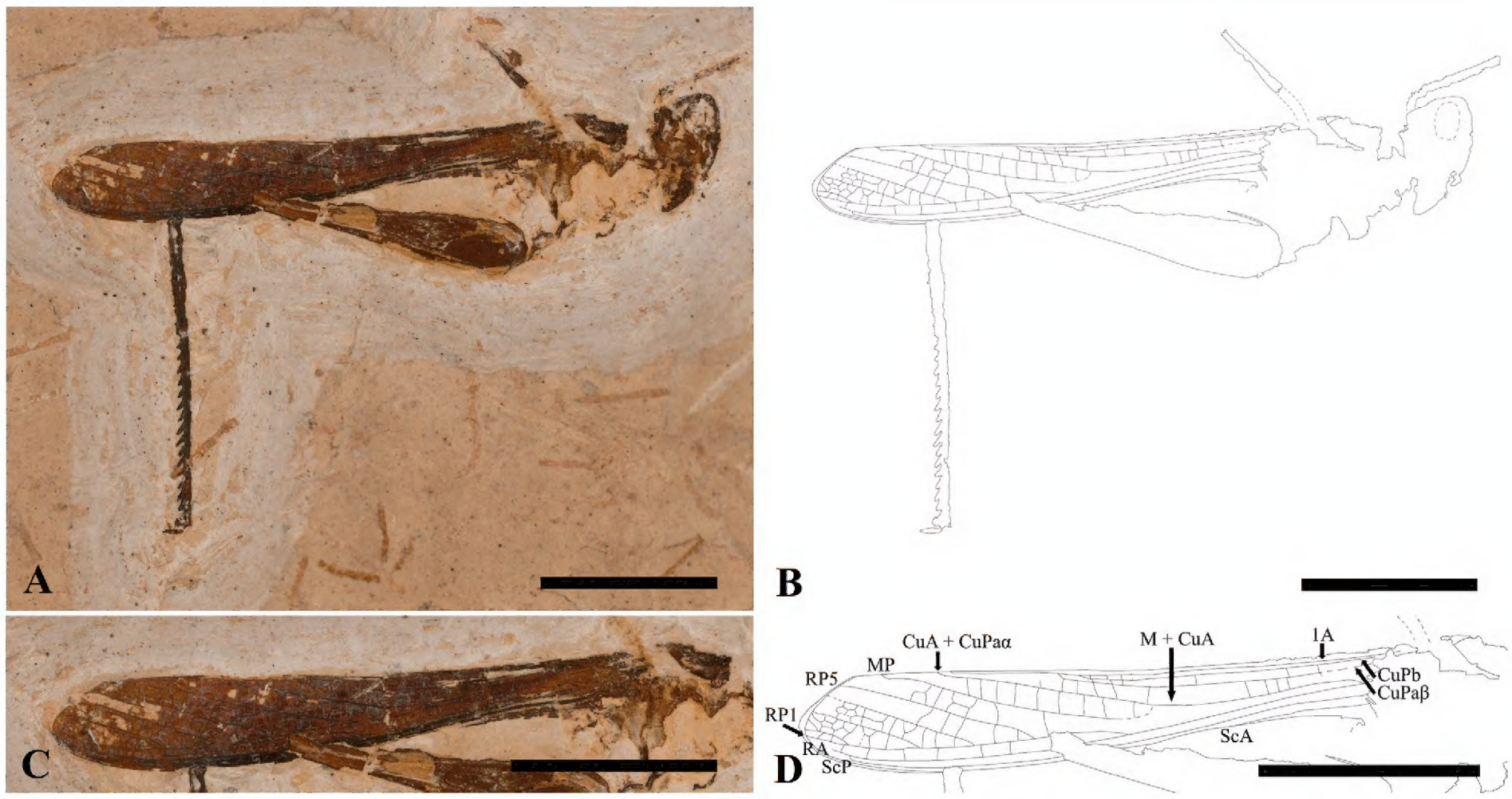

Figure 2. *Cratomastax mariellaae* gen. et sp. nov. holotype (sex unknown), coll. no. MPSC 9664. **A, B.** Image and schematic drawing of the holotype, respectively; **C, D.** Detail and schematic drawing of the wings. Scale bars: 10 mm.

between RP branches, especially distally where it becomes a more complex net pattern.

Head. 6.67 mm high and 3.96 mm wide at widest point (at mid-eye level). Fastigium not prolonged. Antennae not preserved. Eye height ca. 2.09 mm, oval shape, not protruding above head height.

Metathoracic leg. 19.8 mm long, 3.54 mm wide (widest point). Metatibia at least 19 mm long (broken off distally), 0.81 mm wide (widest point). A single row of spines is visible on the dorsal margin of the metatibia, consisting of 16 preserved spines. Spines vary in (preserved) length between 0.18 (first preserved spine) and 0.83 mm (spine at middle). Tarsus not preserved, except for possible fragment at distal end of preserved tibia.

Remarks. Among known fossil species of Eumastacoidea, *Cratomastax mariellaae* sp. nov. most closely resembles *Paleochina duvergeri* and *P. minuta* from the Early Cenozoic of France, although it is closer in size to *P. duvergeri*. *Cratomastax mariellaae* differs from *P. duvergeri* by its larger forewing length (30.2 mm vs. 23.3 mm in *P. duvergeri*), a different forewing length-to-height ratio (7.0 to 8.6), and a narrower spacing between CuPaβ and CuPb. The presence of a eumastacoid in the Crato Formation is not unexpected, although this is the first species to be formally described. Martins-Neto (1991) had already suggested the presence of such forms based on preliminary observations of undetermined specimens. Today, several subfamilies of Eumastacidae Burr, 1899, are represented in the modern faunas of Brazil and surrounding countries. In contrast, Chorotypidae are absent from the extant South American fauna and are currently restricted to Africa and Southeast Asia (Cigliano et al. 2025).

Superfamily Locustopsoidea Handlirsch, 1906
Family Locustopsidae Handlirsch, 1906
Subfamily Pseudoacridinae Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, submitted

Genus *Aestuacrida* Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, 2025

Type species. *Aestuacrida stereofemoris* Schall, Lima, Heads, Pinheiro, Kotthoff & Husemann, 2025

Emended diagnosis. Two branches of M and four branches of CuA + CuPaα (after Schall et al. 2025). CuA + CuPaα do not terminate at fusion to CuPaβ (which, if present, looks like a cross vein), but near wing base.

***Aestuacrida mikronaulion* sp. nov.**
https://zoobank.org/11D2B385-5E07-44D2-81ED-2F4822A87E59
Fig. 3

Etymology. The species name is a combination of the Ancient Greek *mikron* (small) and *aulion* (farm), dedicated to Dr. Ulrich Kotthoff (Leibniz-Institute for the Analysis of Biodiversity Change, Hamburg), who has co-authored several studies on fossil Orthoptera with the first author.

Locality and horizon. Type locality imprecise; from one of the several quarries in the region of Nova Olinda and Santana do Cariri municipalities, Ceará State, Brazil. Nova Olinda Member, Crato Formation, Santana Group. Early Cretaceous, Aptian.

Holotype. Male specimen in the collection of Museu de Paleontologia Plácido Cidade Nuvens, Universidade Regional do Cariri, Santana do Cariri, Ceará, Brazil, coll.

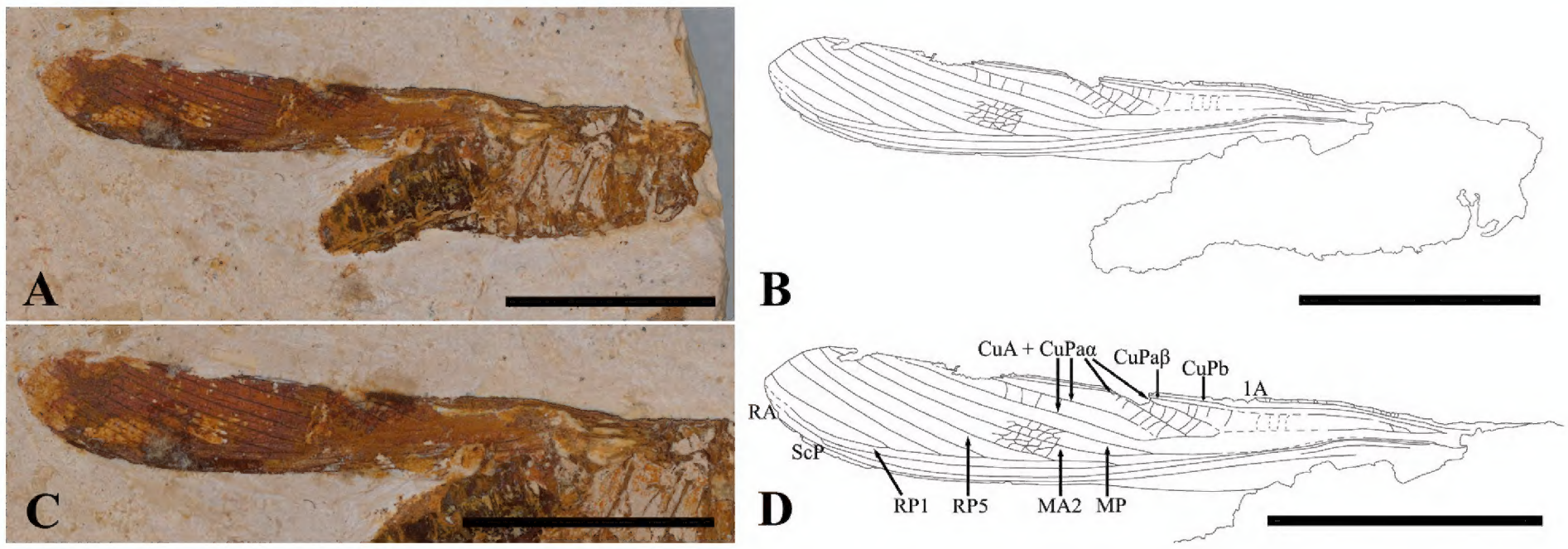

Figure 3. *Aestuacrida mikronaulion* sp. nov. holotype male, coll. no. MPSC 9665. **A, B.** Image and schematic drawing of the holotype, respectively; **C, D.** Detail and schematic drawing of the wings. Scale bars: 10 mm.

no. MPSC 9665. Donation from the Private Collection of Prof. Dr. Martin Husemann (collection number MH_Fossil_0075) as part of the guidelines discussed at the "Brazil-German Colloquium on Paleontology: Science, Cooperation, and Diplomacy for the Future."

Diagnosis. Generic characters (see above). Forewing: RP with five branches. Anterior two branches of CuA + CuPaα reaching anal wing margin, posterior two fused to CuPaβ. ScP long and fused to RA. Forewing length 27.9 mm, maximum height 4.8 mm. Body length 19.1 mm, height (measured at wing base) 6.28 mm. Head height 4.8 mm.

Description. Preservation of wings and body without legs (or the legs are pressed to the body and hardly visible). Measurements of the body and head are given under diagnosis of species.

Forewing. Length/height-ratio 5.8. ScP long and narrow, 92.15% of total wing length (twl). ScP distally with slight upwards path, fused to RA. Space between ScP and RA 7.9% of total wing height (measured at origin of RP3). Origin of RP at 53.9% of twl, posterior to bifurcation of M. Space between RA and RP 7.9% of wing height (measured at same point as before). RP with five branches. M with two branches; bifurcation of M at 49.1% of twl. MA2 reaching anal wing margin at 91.5% of twl. Anterior-most branch of CuA + CuPaα reaching anal wing margin at 82.9% of twl. MP reaching anal wing margin in the middle of MA2 and anterior branch of CuA + CuPaα (precise reaching point damaged). Branches of RP up to first two anterior branches of CuA + CuPaα more or less parallel. Posterior two branches of CuA + CuPaα fused to CuPaβ at 55.3% and 49.8% of twl, respectively. CuPaβ and CuPb long, parallel, and with narrow space in between. 1A relatively short, reaching anal wing margin after 35.8% of twl. Cross vein pattern simple between cubital branches and more complex net pattern between branches of M and RP.

Remarks. *Aestuacrida mikronaulion* sp. nov. differs from its congeneric species *A. stereofemoris* mainly by being significantly larger (forewing length 27.9 mm vs. 16 mm; body length 19.1 mm vs. 12.9 mm). This size difference is unlikely to result from sexual dimorphism, as both known specimens of *Aestuacrida* are probably males. In the new species, the pathing of CuA + CuPaα can be observed, which was obscured in the holotype of *A. stereofemoris*. The absence of fusion between CuA + CuPaα and CuPaβ and the continuation of CuA + CuPaα toward the wing base support the placement of *Aestuacrida* within Pseudoacridinae. However, the genus differs from *Pseudoacrida* Lin, 1982, in having one fewer branch of M and three additional branches of CuA + CuPaα. It can also be distinguished from *Auroralocusta* Schall, Lima, Kotthoff, Pinheiro, Heads & Husemann, submitted, by having three more branches of CuA + CuPaα. The addition of *Aestuacrida* to Pseudoacridinae reinforces the exceptional taxonomic diversity of Locustopsidae in the Crato Formation. Notably, two of the three currently recognized genera within the subfamily—*Aestuacrida* and *Auroralocusta*—are endemic to this deposit.

Subfamily Locustopsinae Handlirsch, 1906

Genus *Locustrix* Martins-Neto, 2003

Species included. *Locustrix audax* Martins-Neto, 2003; *Locustrix gallegoi* Martins-Neto, 2003 (type species).

Diagnosis. Following Martins-Neto (2003), the genus is diagnosed by a short ScP, MA (= M, consisting of MP and MA) two-branched, MP + CuA (= CuA + CuPaα) two-branched and fore- and hindwings with RP three-branched. This diagnosis is herein confirmed. It is possible that the new specimen of *Locustrix gallegoi* described below has RP of the forewing with four branches instead of three, but preservation of venation features in the most distal part of the specimen's wings is not ideal.

Remarks. The new specimen is attributed to *Locustrix* based on the short ScP, as well as the presence of two branches in both M and CuA + CuPaα, all observed in the forewing. Although Martins-Neto (2003) illus-

trated the CuA + CuPaα vein in both original *Locustrix* specimens as single-branched, the generic diagnosis explicitly states the presence of two branches. *Locustrix* can be separated from *Cratolocustopsis* Martins-Neto, 2003—another genus exhibiting two branches of M and CuA + CuPaα—by the markedly shorter ScP in the forewing. In *Cratolocustopsis*, the ScP is of typical locustopsid length, reaching close to the wing apex. *Locustrix* can be assigned to the subfamily Locustopsinae based on forewing venation features—namely, the presence of more than one branch of M and CuA + CuPaα not extending beyond its connection with CuPaβ. Gorochov et al. (2006) tentatively suggested that *Locustrix* may belong to an undescribed subfamily of Locustopsidae characterized by a shortened ScP. However, based on the evidence currently available, we consider that the abbreviated ScP is better interpreted as a genus-level diagnostic feature. Given the limited number of specimens (n = 3), no additional characters currently support the recognition of *Locustrix* as representing a distinct subfamily. This interpretation may be revised should further material become available in the future.

Locustrix gallegoi Martins-Neto, 2003

Fig. 4

Material examined. Male specimen (not of the type series) in the collection of the State Museum for Natural History Karlsruhe, collection number SMNK-PAL 76082.

Remarks. *Locustrix* was established by Martins-Neto (2003) based on two specimens, with the description of two species: *L. gallegoi*, the type species, and *L. audax*. *Locustrix audax* differs from *L. gallegoi* by having a longer ScP reaching the costal margin posterior to the origin of RP, anterior in *L. gallegoi*, and by the bifurcation point of M posterior to the RP origin, anterior in *L. gallegoi*. At the species level, the new specimen can be assigned to *L. gallegoi* based on the shared position of the ScP termination and the anterior location of the M bifurcation point relative to RP.

Discussion

The new species of Eumastacoidea and Locustopsidae described in this study further highlight the diversity of the suborder Caelifera present in the Early Cretaceous of Brazil. *Cratomastax mariellaae* gen. et sp. nov. is the first proof that early eumastacoids were present in this time and area among the much more speciose locustopsids (26 species of Locustopsidae have been described from the Crato Formation, including the new species *Aestuacrida mikronaulion* from this study). Unfortunately, the taxonomy of Locustopsidae and Eumastacoidea is insufficiently understood. A lack of defined apomorphies based on morphological aspects observable in fossils of Eumastacoidea means that all classifications to the family level should be considered with caution (Husemann et al. 2025). Likewise, no clear apomorphies have yet been defined for Locustopsidae (Nel and Jouault 2022). This is bothersome, because this group likely holds a key role in the evolution of Caelifera, possibly as an ancient sister lineage or "ancestors" of the extant Acridomorpha (Gorochov 1995). If early acridomorphs, such as the Cretaceous Eumastacoidea, share a common ancestor with Locustopsidae, then the definition of clear apomorphies to separate both groups and date the origin of Eumastacoidea and extant Acridomorpha is essential. Hopefully, in the future, more well-preserved specimens of both taxa will shed more light on this issue and allow for a more comprehensive understanding of Caelifera evolution, one of the most charismatic suborders in hemimetabolous insect evolution.

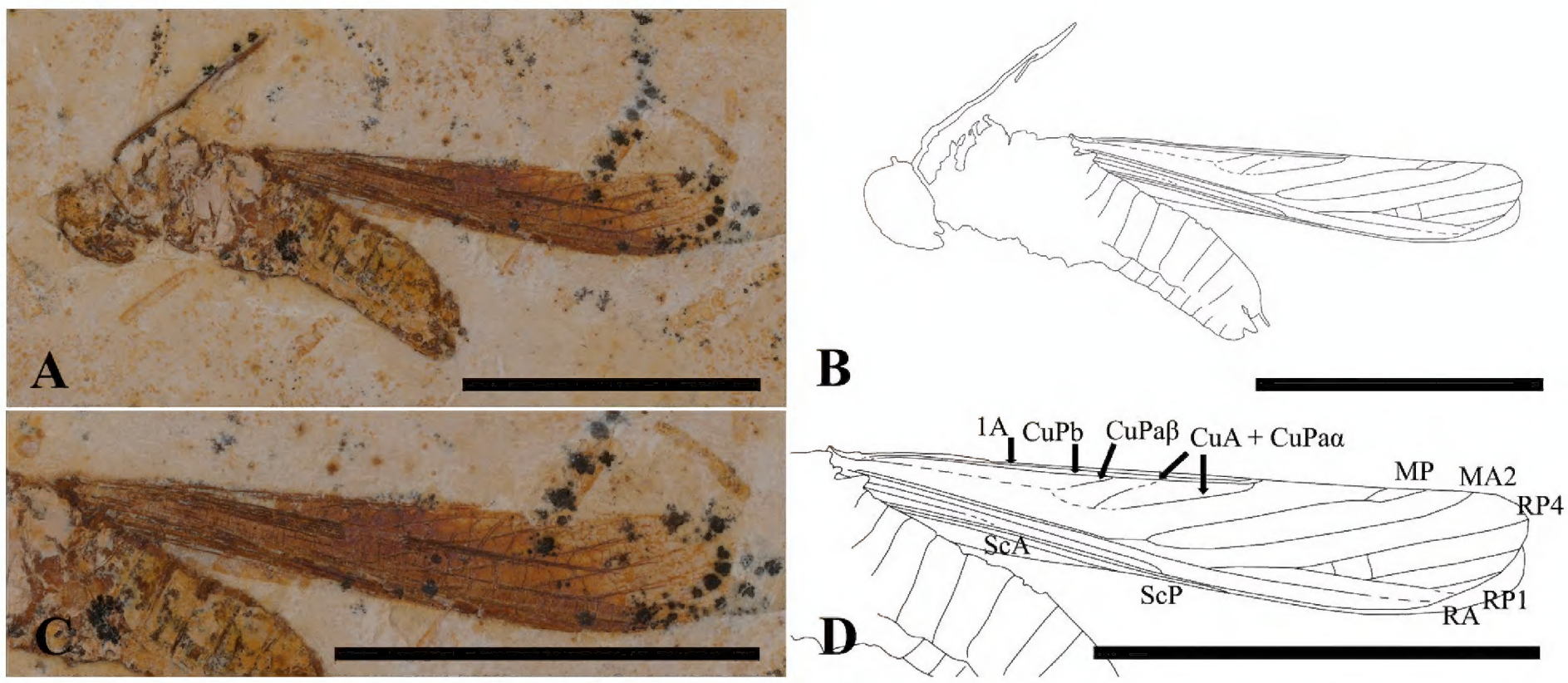

Figure 4. *Locustrix gallegoi* Martins-Neto, 2003. Male specimen, coll. no. SMNK-PAL 76082, not a type. **A, B.** Image and schematic drawing of the specimen, respectively; **C, D.** Detail and schematic drawing of the wings. Scale bars: 10 mm.

Comment on nomenclatural change after a most recent study by Schall et al.

In a recent study published in the journal *Zootaxa* on 21 November 2025, titled "New species of Cretaceous Locustopsidae (Orthoptera: Caelifera) from the Crato Formation of Brazil and a taxonomic revision of the family," by the authors of the present article and Dr. Ulrich Kotthoff, the authors considered the Chinese species *Sinolocustopsis elongatus* Huang & Nel, 2024, to belong in *Locustopsis* as *Locustopsis elongata* (Huang & Nel, 2024). After publication of this article, Dr. Holger Braun kindly reached out to the first author and suggested that a replacement name is needed for *Locustopsis elongata* (Huang and Nel 2024) due to its status as a secondary homonym of *Locustopsis elongata* Handlirsch, 1906, which was considered a synonym of *L. elegans* Handlirsch, 1906, in the publication by Schall et al. (2025). We therefore propose the replacement name *Locustopsis sinensis* (Huang and Nel 2024) for this taxon, named after the Latin "Sino" for Chinese, the place of origin of the species, and after the original name that was given to the genus *Sinolocustopsis* Huang & Nel, 2024. This nomenclatural change is in accordance with Article 57.3.1 of the Code.

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